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SUCCESSION AND RANGE OF MESOZOIC AND TERTIARY FLORAS[1]

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X

It is of course a truism to say that the transition from the Paleozoic to the Mesozoic is not, as was once supposed, an abrupt or catastrophic change, but was brought about so gradually that in many parts of the world it is often difficult, if not indeed impossible, to draw any sharp lines. Not only are the rocks lithologically similar, but a certain percentage of life-forms persisted from the one to the other, yet when each system is considered in its entirety there are apparent abundant lithologic and strongly marked biologic differences. It is my purpose to speak briefly of the floras, first of the Mesozoic and later of the Tertiary.

Triassic.—Rocks of Triassic age are known in many parts of the world and indicate two types of deposition, a fresh-water, marsh, or lagoon phase, and a marine phase. The former is only, or largely, that which has afforded a flora. The known plants of the Trias are relatively few in number. In North America we have less than 150 species, and the entire Triassic flora probably does not exceed 300 or 400 forms. Owing to considerations, physical and otherwise, concerning which there is not complete agreement, the lower portions

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of the Trias afford but scanty remains, and it is not until we come to the upper portion, or Rhaetic, that it can really be dignified as a flora. Our North American Triassic flora is believed to belong largely to this portion. Triassic plants have been doubtfully reported from Prince Edward Island, but they are so obviously of Permian types that they may be disregarded. The principal areas are in North Carolina, Virginia, and Pennsylvania, with relatively few in Maryland, New Jersey, Connecticut, and Massachusetts. In the west we have a doubtful plant or two from Wyoming, a considerable number from northern New Mexico, the extensive fossil forests of Arizona, and a very few species from Plumas County, California. Going southward we have small collections from Sonora, from about the City of Mexico, in Honduras, Chile, and western Argentina. In other parts of the world Triassic floras have been found in England, east coast of Greenland, Spitzbergen, North Germany, southern Sweden, Italy, southwestern Spain, Persia, India, China, Tonkin, Japan, New South Wales, New Zealand, and South Africa.

What, now, are the characters of the Triassic flora? The dominant types of the Paleozoic have largely disappeared. The Lepidodendrae, Sigillariae, Calamites, Cordaites, Sphenophyllae, and Cycadofilices, so far as ascertained, have all gone, as well as a number of important genera of ferns—*Cheilanthites*, *Mariopteris*, *Megalopteris*, etc. The most notable survival from the Paleozoic is the so-called *Glossopteris* flora, which has been found with a few associated forms in Rhaetic rocks at Tonkin, the Stormberg series of South Africa, New South Wales, etc.

The Triassic flora consists essentially of equisetums, ferns, cycads, and conifers of many genera. A few forms such as *Ginkgo*, *Cladophlebis*, *Thinnfeldia*, etc., had a small beginning in the Paleozoic and expanded in the Mesozoic into large groups. But most of the flora is of distinctly Mesozoic and northern origin.

It has often been said that the plants of the Triassic are depauperate and pinched in aspect, indicating unfavorable climatic conditions. The paleobotanical facts do not altogether bear this out. In North Carolina, Virginia, and Arizona, there are trunks of trees preserved, some of which are 8 feet in diameter and at least 120 feet long, while hundreds are from 2 to 4 feet in diameter. Many of the

ferns are of large size, indicating luxuriant growth, while Equisetum stems 4 to 5 inches in diameter are only approached by a single living South American species. The cycads are not more depauperate than those of subsequent horizons, nor do they compare unfavorably with the living representatives.

The complete, or nearly complete absence of rings in the tree trunks indicate that there were no, or but slight, seasonal changes due to alternations of hot and cold, or wet and dry periods. The accumulations of coal—in the Virginia area aggregating 30 to 40 feet in thickness—indicate long-continued swamp or marsh conditions, while the presence of ferns, some of them tree-ferns, indicate on the whole a moist, warm, probably at least sub-tropical climate.

Jurassic.—Coming, now, to the Jurassic, we find in the lower portion indications of a continuation of conditions which obtained in the upper portions of the Trias. The distinctive Paleozoic elements had finally disappeared, and the Mesozoic life-forms were in full swing, expanding in the middle and upper parts of the period into the abundant and widespread flora as we know it. In fact the relative uniformity and wide extension of the Middle and Upper Jurassic flora is one of the most interesting and impressive exhibits that we have. (See map showing approximate distribution of Triassic and Jurassic flora.)

There is no paleobotanical evidence indicating the presence of the Jurassic in Eastern North America. In the western interior Jurassic plant-bearing beds occur in the Black Hills, South Dakota, and the Freezeout Hills, Carbon County, Wyoming. We then pass to the Pacific coast, where we have a fine flora near Oroville, California; also northward in Trinity and Tehama counties, California, and Douglas and Curry counties, Oregon.

The following is an outline of the world distribution of the flora:

Alaska	Copper River District
	Cook Inlet
	Herendeen Bay
	Cape Lisburne
England	Yorkshire
France	Mamers—northwestern portion
Germany	Franco-Swabian area
	Northwestern area

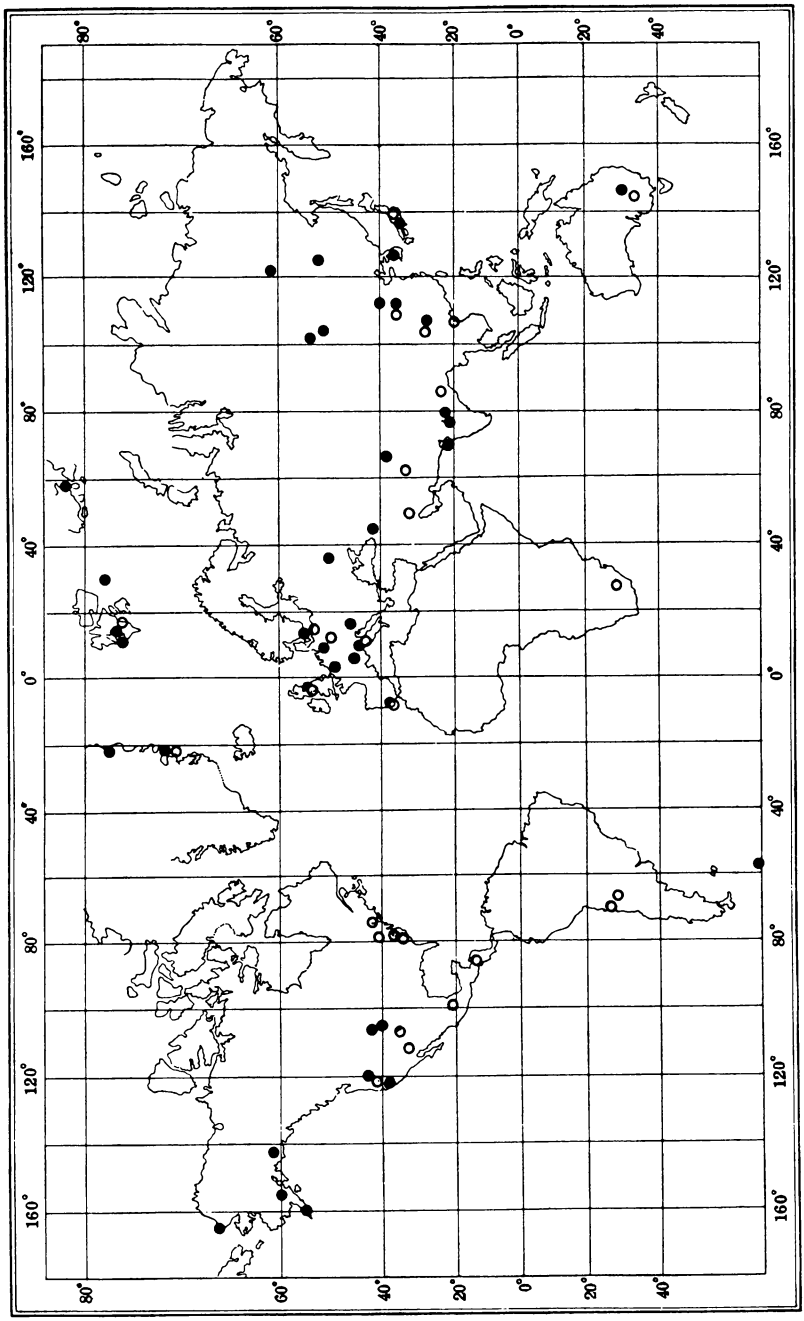

FIG. 1.—Map showing approximate distribution of Triassic and Jurassic floras.

Rings = Triassic
Dots = Jurassic

Austria-Hungary	Steierdorf in Banat
	Crojie in Galicia
	Cracow
Italy	
Switzerland	
Portugal	
Sweden	Bornholm
	Bjuf
Spitzbergen	Cape Boheman, 78° −22′ N.
	Advent Bay, Cape Staratschin
	Green Harbor
King Karls Land	78–79° N.
Franz Josef Land	82° N.
Greenland	Cape Stewart
	80° N.
Siberia	Ust-Balei 51° N.
	Irkutsk
	Upper Armour River
	Lena River District
Corea	
Japan	
Caucasia	
Turkestan	
India	Cutch
	Jabalpur
China	Tyrkyp-Tag
	Border Hami Desert
Australia	
New Zealand	
Louis Philippe Land	63° S.

The flora of the Jurassic, while in the main a continuation of that of the late Trias, and consisting of equisetums, ferns, cycads, ginkgos, and conifers, shows the incoming of a number of more modern types in these groups. The cycads were of course abundant and diversified, whence it has been called the age of cycads. The flora is remarkably uniform over wide portions of the world. Thus not far from 50 per cent. of the North American flora—exclusive of the cycad trunks—is the same as that found in Japan, Manchuria, Siberia, Spitzbergen, Scandinavia, or England, and what is even more remarkable, the plants found in Louis Philippe Land, 63° S., are practically the same as those from Yorkshire, England.

Some idea of the climatic conditions which prevailed at this time may be gained from the present distribution of certain obvious descendants of the Jurassic flora. Thus *Matonidium* and *Laccopteris* are represented by *Matonia* of which there are two species living in the Malay region and Borneo; *Dictyophyllum*, *Protorhipis*, *Hausmannia*, *Caulopteris*, etc., are closely allied to *Dipteris*, which has five species living in the eastern tropics; Ginkgo—so abundant in the Jurassic—has but a single living representative in China and Japan.

Climatic conditions in Jurassic.—The presence of luxuriant ferns, many of them tree-ferns, equisetums of large size, conifers, the descendants of which are now found in southern lands, all point to a moist, warm, probably subtropical climate, though in late Jurassic time the presence of well-defined rings in the tree trunks of species found in northern areas—King Karl's Land, Spitzbergen, etc.—show that there were beginning to be sharply marked seasons.

Wealden.—Immediately above what by common consent is regarded as the top of the Jurassic, is a series of fresh-water plant-bearing beds that are of quite wide extent in this country, though different names have been applied in the different areas. Thus the lower Potomac of the eastern United States (including the Patuxent and probably Arundel), the Glen Rose beds of the Trinity division of Texas, the Lakota and Cloverly of Dakota and Wyoming, the Kootanie of Alberta and adjacent Montana and extending into the Bighorn Basin of Wyoming, and the Shasta of California, and Kome of Greenland are practically equivalent in age, and correspond most closely in age with the Wealden of the Old World, which is considered to be a fluviatile or lacustrine condition of the lower Neocomian, the lowest member of the Cretaceous. The flora is a comparatively rich one, aggregating between two hundred to three hundred species, and is composed of ferns and conifers with a fair sprinkling of cycads Equisetaceae, ginkgos, etc. It shows a considerable agreement with the Jurassic, a number of species being common to the two, but on the whole its affinity is rather with the Cretaceous.

Cretaceous.—Up to the present point in the geological column the most characteristic and dominant feature of the modern flora—namely the angiosperms—has been absent. In many ways the introduc-

tion of this type of vegetation was one of the most important and far-reaching biologic events the world has known. For many years the flora of the Dakota Group and kindred floras was the oldest angiospermous flora known in this country, but as there are such a host of apparently modern types present, it was presumed that they must have had an ulterior period of development—and such proved to be the case. So far as we now know this flora appears to have had its origin in eastern or northeastern North America, in the Patapsco division of the Potomac series. Although the great majority of the plants found in association in these beds, both as regards species and individuals, still belonged to lower Mesozoic types, such as ferns, cycads, and conifers, we find ancient if not really ancestral angiosperms, and many of the same types are found in beds of approximately the same age (that is Albian) at Circal in Portugal. Although we are here much nearer the origin of the angiosperms than was before known, we are probably still some distance from their actual point of origin, but just where or when that was we do not, and may never know.

No sooner were they fairly introduced, however, than they multiplied with astonishing rapidity and in the upper members of the Potomac series—Raritan—they had become dominant, the ferns and cycads having mostly disappeared and the conifers having taken a subordinate position.

By the close of the Comanchan, or Lower Cretaceous, they had spread as far north as Alaska and Greenland, and a large number of modern genera were established.

Climatic conditions during Comanchan.—The climate over this vast area was certainly much milder than at the present time, for such well-known plants as elms, oaks, maples, magnolias, and many others were growing 72° N., in Greenland and nearly as far north in Alaska. It was at least what we would now call warm temperate.

Upper Cretaceous.—With the inauguration of the Upper Cretaceous the angiospermous flora was in full swing.

On the Atlantic border we have the Magothy, which extended from Maryland over New York, Long Island, and as far as Martha's Vineyard. The flora is a rich one, embracing about one hundred and fifty species.

In the interior, in approximately the same position, is the Dakota,

which has afforded a splendid flora of over five hundred species, and occurs in Kansas, Nebraska, Wyoming, Minnesota, along the international boundary, and some of the same forms as far as central Alaska and south to Argentina.

Of the succeeding members of the Upper Cretaceous the Colorado being largely marine has but a small flora, although in southwestern Wyoming there is a small flora, made up mainly of modern types of ferns (*Gleichenia*), that finds its closest affinity in the Upper Cretaceous of Greenland.

Montana.—As this represents alternations of marine with brackish- and fresh-water conditions we have a larger flora, although the total number of known species probably does not exceed one hundred and fifty. Nothing particularly new was established at this time, the genera there being largely of older formations, though the species are mainly different.

Laramie.—As the uppermost member of the Cretaceous series above the marine Fox Hills, the Laramie has had many vicissitudes of interpretation and was made to include beds now known to belong to the Montana, Arapahoe, Denver, Fort Union, etc. As logically restricted to the original definition of King, the plant-bearing Laramie is confined largely to the Denver Basin of Colorado and adjacent areas to the southward, with the probability of its being demonstrated to exist west of the mountains in Colorado, Wyoming, and New Mexico. As above restricted the Laramie flora comprises about one hundred and twenty-five species, and proves to be remarkably distinct from that of the Montana below as well as from the Arapahoe, Denver, and Fort Union above.

Tertiary.—The close of the Upper Cretaceous saw a considerable percentage of the modern angiospermous types of vegetation fully established, not only in North America but throughout the world, and the ferns, cycads, and conifers relegated permanently to a subordinate position. Certain types of dicotyledons, such, for instance, as magnolias, tulip-trees, sassafras trees, etc., had their maximum development in the Cretaceous, and in the Eocene and subsequent stage were greatly reduced until in the modern flora they are often represented by a few or even single species of very restricted habitat. The most noticeable feature of the Eocene flora, broadly considered,

is the increased number of forms that foreshadow the modern flora, a few, indeed, being still living. As examples of the latter mention may be made of the common sensitive fern (*Onoclea*) and two species of hazelnut (*Corylus*) all of which are now living in eastern North America. In late Cretaceous time the sedges (*Cyperus, Carex*, etc.) and grasses (*Arundo, Phragmites*) had but a poor representation, but in the late Eocene these groups clearly became more numerously developed both in types and species, and thus apparently made possible the rise and development of the mammalia.

Fort Union flora.—The largest and in many respects most important Eocene flora is that of the Fort Union, which is found over a vast area in the central Canadian provinces, north as far as the valley of the Mackenzie River, and south over central and eastern Montana, the western portions of both North and South Dakota, and at many points in eastern and central Wyoming and northwestern Colorado. It has recently been shown by the writer[1] that the Fort Union, extensive as it was known to be, really embraces more than has commonly been assigned to it. Conformably underlying the beds by some geologists considered as the true Fort Union, occur beds which have often been incorrectly referred to the Laramie, or its equivalents, but which are now regarded as constituting the lower member of the Fort Union formation. This lower member, which includes the so-called "Hell Creek beds" and "somber beds" of Montana, and the "Ceratops beds" of Wyoming, and their equivalents throughout much of the area above outlined, contains a rich flora which is inseparably bound to the flora of the upper member.

The flora of the Fort Union considered as a whole embraces more than five hundred species, and comprises ferns, sequoias, cedars, yews, grasses, sedges, oaks, willows, poplars in great abundance and variety, hazelnuts, walnuts, elms, sycamores, maples, a few figs, an occasional palm, and other more modern types. Whatever the conditions under which this flora grew and was entombed, it is beyond question that the climatic conditions were very different from those now prevailing in the region. But for the presence of palms and an occasional fig it might be presumed that the conditions were not greatly different from those now experienced in Atlantic North Amer-

[1] *Proc. Wash. Acad. Sci.*, Vol. XI, 1909, pp. 179–238.

ica, that is, cool temperate. This flora, which is closely similar to that in north Greenland and the valley of the Mackenzie River, undoubtedly approached from the north. The presence of palms, which are found in the lower parts of the formation, argues, on the basis of present distribution, a somewhat warmer climate, just as the numerous thick beds of lignite throughout the formation argue for extensive, long-continued, moister, marsh conditions.

The flora of the lower member of the Fort Union as at present elaborated embraces about eighty-five species of which number about sixty-five are found in the upper member, while only sixteen of the eighty-five species are found in the Cretaceous below. The uncomformity of the base of these beds together with the differences in the flora, clearly and logically marks the point at which the line is to be drawn between Cretaceous and Tertiary.

In the Mississippian region in Louisiana and Mississippi we have a small Eocene flora (Eolignitic) comprising palms, evergreen oaks, magnolias, laurels, cinnamomums, etc., which appear to be most closely affiliated with small floras in northern New Mexico and adjacent Colorado, the latter in turn being most closely related to much larger post-Laramie floras in the Denver Basin of Colorado. These embrace the Arapahoe with about thirty species, and the Denver with nearly two hundred species, and are believed to be slightly older than the Fort Union—in any event, there are only about thirty species in common.

The Green River formation of upper Eocene age occupies a quite extensive area in central and western Wyoming, and has afforded a flora of some eighty species. It is very distinct from the Fort Union and other Lower Eocene floras, and shows a distinct increase of modern forms.

In the northern Pacific coast region there are a number of Eocene floras, among them that of the Swauk which occurs just east of the Cascade Mountains in Washington. This large flora is entirely different from any other in this country, and consists of types that are for the most part found in Central and northern South America, among them being palms 6 feet in diameter and in layers sometimes a foot in thickness. This shows that the palms were not sporadic or occasional, and indicates, as do many of the other things, that the

climate was mild, probably subtropical. The overlying Roslin formation contains a flora that is almost entirely different from that of the Swauk, and lacking the presence of palms was probably slightly cooler than the underlying formation.

To the northward and covering a vast area in Alaska and well out on the Alaskan peninsula is the Upper Eocene Kenai formation which has afforded a rich flora of oaks, poplars, willows, hazels, walnuts, magnolias, horse-chestnuts, and maples, together with pines, spruces, cedars, and sequoias. This flora is found in British Columbia, and abundantly in Greenland, Iceland, and Spitzbergen, showing that it was of wide extent in similar northern latitudes. It is distinctly a warm-temperate flora. Another Upper Eocene flora is found in the Clarno formation of the John Day Basin, Oregon, and in the Payette formation of western Idaho. It embraces walnuts, hazels, birches, alders, oaks, elms, sycamores, maples, ashes, etc., and is temperate or warm temperate, in character.

Eocene floras in the Atlantic area are of very little importance as thus far developed.

Miocene.—The Miocene flora of North America is relatively not a large one although it comprises probably five hundred species as now known. The deposits occur often in isolated basins, widely separated, and there is usually comparatively little in common between them. A number of the more important areas may be briefly mentioned.

At Brandon, Vermont, in the midst of ancient crystalline rocks, occur small pocket-like deposits of lignite which have yielded large numbers of fossil fruits and a very few poorly preserved leaves. The fruits have been studied by Lesquereux, Perkins, and others, and about one hundred and fifty nominal species described belonging to the genera *Nyssa*, *Hicoria*, *Juglans*, *Bicarpellites*, *Cucumites*, *Tricarpellites*, etc.

At Florissant, Colorado, also in the midst of older rocks, there are small lake-bed deposits which have afforded vast quantities of plant and insect material in an admirable state of preservation. The plants number upward of two hundred species, among them being a great number of very modern types and even including not a few herbaceous forms. This flora as a whole is very unlike anything

found in the region at the present day and apparently finds its closest affinity with the West Indies, though doubtless it also approached originally from the north.

Small deposits containing a Miocene flora have been found in Esmeralda County, Nevada, the Similkameen Valley, and other points in British Columbia, and in the Yellowstone National Park. The so-called Muscall beds of the John Day Basin, Oregon, and extending into central Washington, have yielded a rich flora of about eighty species, among them oaks, maples, poplars, barberry, bread-fruit trees, etc., indicating a warm, moist climate. Associated with the auriferous gravels of California is a flora of about one hundred and twenty-five species, some of which are of very modern appearance, such as *Zizyphus*, *Magnolia*, *Persea*, *Acer*, *Artocarpus*, etc.

Pliocene.—The Pliocene flora of North America is almost a negligible quantity, about the only known locality being the Falls of the Columbia River. It includes species in the genera *Woodwardia*, *Sassafras*,*Sterculia*, etc., and is very closely related to living American species.

Pleistocene.—The Pleistocene flora is better known than the last, yet we are undoubtedly only on the borderland of a knowledge of the plants of this period and their distribution. Small Pleistocene floras are known from New Jersey, Maryland, Virginia, West Virginia, North Carolina, Alabama, New York, Iowa, and Canada. The most extensive exploitation of this flora is that made in Canada in the vicinity of Montreal and Toronto, where Penhallow has been able to make out at least three stages. The species are nearly all living.